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EFFECTS OF FOODRESOURCE LEVELS
ON
TUNDRA BIRD POPULATIONS

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I. SUMMARY

The nine most common nesting bird species on the tundra at Prudhoe Bay consist of eight shorebirds and one passerine, the Lapland Longspur. Studies of the diets of these species at other arctic tundra sites (principally Barrow) have shown that insects comprise their principal prey during the breeding season. Diets differ somewhat among species, but the relatively simple prey base at arctic sites results in broad diet overlap. All species exhibit pronounced seasonality in their diets, responding to seasonal variation in availability of their prey. Most species rely on larvae of tipulid and chironomid flies in June, switching in July to emerging adults of these dipteran families. In late summer, after emergence is complete, most birds return to larval dipterans. Spiders, beetles and other insects are occasionally important. A few species take berries and plant seeds before or after the nesting period.

Potential effects of West Road on food supplies of tundra birds include gross habitat changes as well as subtler effects such as road dust and changes in snow melt. Aside from gravel burial, the most drastic effects will involve drainage changes (impoundments) which may alter insect species, densities, seasonality, and availability to birds. Dust and resultant snow melt changes might alter vegetation and soil texture, chemistry, and moisture, changing the environment of soil invertebrates. This could cause similar but less marked changes in insect species, densities and phenology.

Tundra bird densities may be limited by food (insect densities) on several scales of area, from single territories to regional sites, but the limitation is probably based on an average of food densities over several years. Differences among potentially competing species in site philopatry and annual variability in numbers complicates this question. Some studies of shorebird ecology on summer and winter grounds have suggested that competition is more important in winter, and that breeding ground resources are abundant and not limiting. This apparent contradiction can be reconciled by considering population relationships between summer and winter, differences in diversity of seasonal prey base, and differences in the nature of potential food limitation between

summer and winter. The issue is complex and not easily solved, but the evidence suggests that food supplies are involved in setting local breeding densities on the tundra.

I discuss four approaches to studying the effects of West Road on bird densities through changes in insect densities. Two of these are more promising in terms of time and effort required. A restructured monitoring of insect densities, with continued monitoring of bird densities along West Road, is part of this dual approach. Supplementing this, an experimental measurement of effects of lowered insect densities (through increased bird density) on chick growth rates would focus on a key question of whether changes in insect abundance will decrease nesting success.

II. INTRODUCTION

What effects will West Road have on tundra bird populations through changes in their food supplies? To answer this basic question we must focus on three separate questions: What are the important food resources of the most common tundra birds at Prudhoe Bay? What are the probable effects of West Road on these food resources? Do food resources limit tundra bird populations, such that changes in food densities will produce changes in bird densities? In this report I will address each of these topics and discuss studies which could fill relevant information gaps. I will pay particular attention to the question of food as a resource limiting bird populations, because this is at the heart of the initial question posed, and because this is the most complex and difficult to answer of the three component questions. Finally I will give my reasons for believing that the primary, most easily measured changes in bird populations will arise from gross habitat changes, which necessarily involve changes in food supplies. Changes through effects on food supplies unaccompanied by gross habitat changes may also occur, however, and studies can be focused on these effects.

The Tundra Avifauna

As measured by nest densities, the tundra avifauna at Prudhoe Bay is dominated by several species of shorebirds and one passerine, the Lapland Longspur. From data of Troy and Johnson (1982) on experimental and control transects near West Road, all 9 species with nest densities above 1 per km² are included in this group (see Table 1). The 1981 results compare fairly closely with the most common nesters in 1971 and 1972 on three study plots near Prudhoe Bay (Norton et al 1975). In both studies the three most abundant nesting species were Semipalmated Sandpiper, Red Phalarope and Lapland Longspur, although their relative abundances differed. Dunlin, Pectoral Sandpiper and Northern Phalarope formed the next most abundant group in both studies. These results probably apply to most years and most sites at Prudhoe Bay. Four other shorebirds and one passerine nested on study transects in 1981 at lower densities, as did seven species from other groups, principally waterfowl. (Troy and Johnson 1982). Because of the overwhelming numerical dominance of the shorebirds and passerines in the study area, and be-

cause these species generally share a similar range of habitats and food resources, this report will consider only those species in Table 1.

Table 1. Species nesting on Waterflood Project bird transects, 1981
(from Troy and Johnson 1982).

A. Nesting densities above 1 per km²

Lapland Longspur	<u>Calcarius lapponicus</u>	15.9 nests/km ²
Semipalmated Sandpiper	<u>Calidris pusilla</u>	15.4
Red Phalarope	<u>Phalaropus fulicarius</u>	13.6
Dunlin	<u>Calidris alpina</u>	8.0
Pectoral Sandpiper	<u>C. melanotos</u>	5.4
Northern Phalarope	<u>Phalaropus lobatus</u>	2.4
American Golden Plover	<u>Pluvialis dominica</u>	2.2
Baird's Sandpiper	<u>Calidris bairdii</u>	1.9
Buff-breasted Sandpiper	<u>Tryngites subruficollis</u>	1.3

B. Related species nesting at densities below 1 per km²

Black-bellied Plover	<u>Pluvialis squatarola</u>
Ruddy Turnstone	<u>Arenaria interpres</u>
Long-billed Dowitcher	<u>Limnodromus scolopaceus</u>
Stilt Sandpiper	<u>Calidris himantopus</u>
Snow Bunting	<u>Plectrophenax nivalis</u>

Other nesting species, all at densities below 1 per km², include Arctic Loon, Gavia arctica, Red-throated Loon, Gavia stellata, L'bite-fronted Goose, Anser albifrons, Oldsquaw, Clangula hyemalis, King Eider, Sterna spectabilis, Rock Ptarmigan, Lagopus mutus, and Parasitic Jaeger, Stercorarius parasiticus.

111. FOODS OF TUNDRA BIRDS

Types of Information Available

Diet information for tundra birds is available in a variety of sources ranging from one-sentence lists of food types to detailed analyses of stomach contents of collected birds. These may give results as percent of biomass, percent by number of total prey items, frequency of occurrence in stomachs based only on presence/absence, or frequency of only the most common food items. Samples are sometimes separately analyzed by age and sex, by habitat, by period within a season (by calendar dates, bird breeding phenology or insect phenology), by year and by geographic site; or any of these potential categories may be combined and obscured. *Prey* items may be identified to species and to size, or they may be listed in general taxonomic categories, as families (tipulids), orders (dipterans), or even classes (insects). The result is a wide variation in detail and reliability among sources of diet information, which I will attempt to summarize. This requires dropping much of the detail in favor of extracting the most relevant generalizations regarding each species. Such an approach is appropriate because species diets vary according to the availability of prey: birds can select only among the prey items locally available. Great precision and detail pertaining to one place and time are therefore not normally transferable to other sites, although the general conclusions regarding food types usually are.

Two families of insects within the order Diptera (flies) will be mentioned repeatedly in these discussions: Tipulidae (crane flies) are widespread on arctic tundra, occurring in a variety of upland and low-land habitats. Several species vary in size, but the most common species at Barrow and Prudhoe Bay (Tipula carinifrons and T. arctica) are quite large (more than 10 mg dry weight as larvae; Miles 1966b, Custer and Pitelka 1978, MacLean and Ayres 1982). Their full growth cycle takes up to 4 years to complete. Chironomids (midges) are smaller (less than 1 mg dry weight as larvae), and occur in wet habitats such as pools and edges of streams and lagoons throughout the arctic. Near Barrow and Prudhoe Bay there may be 25 species or more, and life cycles may take up

to seven years to complete (Butler et al 1980). Thorough discussions of the natural history and seasonality of these and other groups of tundra invertebrates can be found in MacLean and Pitelka (1971), MacLean (1980), and MacLean and Ayres (1982).

Species are treated below in order of nesting density in 1981, as listed in Table 1, beginning with the most abundant species.

Lapland Longspur. ---- Tundra diets of this passerine at Barrow have been reported in Custer and Pitelka (1977, 1978) and Seastedt and MacLean (1979). Because the principal large tundra arthropods at Barrow and at Prudhoe Bay are similar (MacLean 1975, 1980, MacLean and Ayres 1982) we can expect Prudhoe diets to be similar in type and seasonality to those measured at Barrow. Adult longspurs feed primarily on larval insects in June, switching to emerging adult insects in July when these become available, and returning to larval insects after emergence is complete (Table 2). On first arrival in late May the tundra is mostly snow covered, and longspurs forage on plant seeds (74%). They shift back toward plant seeds in August (Custer and Pitelka 1978), a trend also suggested by the contents (almost exclusively seeds) of two stomachs of juveniles examined in August (Connors, unpublished) from a saltmarsh area near Barrow.

Table 2. Lapland Longspur diets at Barrow. Percent composition by weight.

A. Adult diets (Custer and Pitelka 1978), n = 174.

	June 1-10	June 11-20	June 21-30	July 1-10	July 11-20	July 21-30	Aug	Summer Average
Larval <u>tipulids</u>	37%	62	34	9	3	13	6	23%
Adult <u>tipulids</u>	3	0	4	68	69	14	2	23
Other <u>larval insects</u>	33	23	20	5	7	52	37	25
Other adult <u>insects, spiders</u>	18	12	28	12	20	14	8	16
Seeds	4	0	4	2	1	4	27	6

B. Nestling diets (Seastedt and MacLean 1979)

Larval tipulids	25%
Adult tipulids	44
Other diptera	10
Other insects	15
Spiders	6

Food fed to nestlings consisted of the same arthropod taxonomic categories: Almost 70% of the biomass consisted of larvae and adults of tipulid flies, with other insects and spiders comprising the remainder of the nestling diet.

Longspur diets from breeding grounds more remote from Prudhoe Bay have also been reported, and the results do not differ importantly from the Barrow studies. Two of these report that seeds comprised about half the diet, but birds were collected throughout the summer in these studies: the averaged results may reflect the spring or late summer use of seeds measured at Barrow. At Cape Thompson in 1960 animal matter in 90 longspur stomachs consisted of beetles, flies, other insects and spiders (Williamson 1968). Nestlings were fed only animal matter, as at Barrow. Gabrielson (1924), reported the contents of 56 stomachs of Lapland Longspurs from Alaska and Northern Canada breeding grounds. Flies, mostly tipulids, were the main animal prey items, but beetles, other insects and spiders were also taken frequently, in addition to seeds.

Timing of longspur nesting differs from that of shorebirds. Longspurs have a shorter incubation period, and their young hatch a week or more before most shorebirds (Holmes and Pitelka 1968, Williamson 1968, MacLean 1969, Custer and Pitelka 1977). The young are altricial, staying at or near the nest, where they are fed by the adults, until they fledge. Shorebird young are precocial, highly mobile and able to forage for their own food within 24 hours of hatching. All these species are very synchronous in timing of their nesting, probably in response to the narrow seasonality of prey abundance upon which they depend, which in turn is set by factors of climate in the brief arctic summer (Holmes and Pitelka 1968, MacLean and Pitelka 1971, Custer and Pitelka 1977, 1978). Holmes and Pitelka (1968) and MacLean and Pitelka (1971) believe that shorebird breeding is timed so that hatching occurs at the beginning of the peak of adult insect emergence, providing an easily caught prey for foraging chicks. Similarly, Custer and Pitelka (1977) suggest that longspur hatching occurs earlier so the young reach independence while adult insects are abundant. As nestlings, they depend on adults who can successfully forage for larval insects before insect adult emergence. This suggests that newly independent young require the easily captured adult insect prey; condition and timing of

food supplies during this period may be critical to longspur success. Marked changes in insect phenology due to effects of West Road on local snow melt could alter the success of longspur (or shorebird) Young if these species cannot adjust their nesting schedules accordingly.

Semipalmated Sandpiper. ---- The most extensive diet information for this species and for three other sandpipers on our list comes from Holmes and Pitelka's (1968) study at Barrow. They collected a total of 694 adult and 372 young sandpipers of four species over a period of five summers. They analyzed this mass of data by ten or fifteen day periods, enabling them to track seasonal changes in species diets averaged over five years at one site. They concluded that all four species feed almost exclusively on insects; that seasonal trends in their diets result primarily from phenology of insect availability; and that all four species overlap broadly in summer diets. Implications of these conclusions will be discussed in subsequent sections of this report.

For Semipalmated Sandpipers, chironomids (midges) are the most important prey throughout the season (Table 3). During June, these sandpipers forage heavily on chironomid larvae in muddy margins of pools, lakes, streams and lagoons. During July adult chironomids emerge abundantly in these habitats and comprise the bulk of Semipalmated Sandpiper diets. As emergence diminishes in mid to late July, the birds switch back to chironomid larvae. Other prey taken in smaller numbers include tipulid larvae and adults, spiders and beetles.

Young sandpipers forage on the same prey, beginning with adult chironomids after hatching in early to mid July, and switching to larvae in late July and early August. At this time many young birds move into coastal areas, foraging on mudflats, salt marshes, and edges of sloughs and lagoons prior to fall migration. Stomachs of six birds collected in these habitats at Barrow and at Lonely, Alaska contained primarily chironomid larvae (73%), but also held oligochaete worms (17%) and chironomid adults (3%) (Connors and Risebrough 1976, 1977).

The Barrow results agree with diet information from the eastern Canadian arctic (Eaker 1977) where a sample of 33 birds (collected mainly in June) contained chironomid larvae (61%), spiders (23%) and small amounts of several other categories, mostly insects. The Semipalmated

Table 3. Diets of Semipalmated Sandpipers at Barrow (from Holmes and Pitelka 1968). Percent composition by number of items.

A. Adults, n=60

	June 1-10	June 11-20	June 21-30	July 1-10	July 11-20	July 21-30	June-July Average
Adult <u>chironomids</u>	0%	4	2	76	35	0	20%
Adult <u>tipulids</u>	0	0	0	14	11	0	4
Larval <u>chironomids</u>	52	50	85	5	49	87	55
Larval <u>tipulids</u>	13	17	9	0	3	0	7
Adult <u>Spiders</u>	16	18	2	1	3	10	8
Adult <u>Beetles</u>	12	12	3	8	4	4	7

B. Young, n=39

	July 1-20	July 11-20	July 21-30	July 31 - Aug. 14	July-Aug. Average
Adult <u>chironomids</u>	84%	56	5	3	37%
Larval <u>chironomids</u>	0	4	81	88	43
Adult <u>Spiders</u>	4	16	1	4	6
Adult <u>Beetles</u>	10	13	6	1	8

Sandpiper is the smallest of the shorebirds nesting at Prudhoe Bay, and both Holmes and Pitelka (1968) and Baker (1973) found differences in sizes of prey selected by this species compared to other sympatric shorebirds. Semipalmated Sandpipers take smaller prey on average but the lack of diversity in its diet and in those of potential competitors still results in broadly overlapping diets among these species.

Red Phalarope. ---- Several observers have reported tundra foods of this species, and almost all observations indicate that insects, primarily chironomids, constitute the bulk of the diet. During most of the year Red Phalaropes feed on marine zooplankton, and many of the tundra ponds where they nest contain similar-sized freshwater zooplankton, but these items have been found in stomachs only infrequently (Sergman et al 1977, Kistchinski and Chernov 1973). This may be in part because the soft-bodied zooplankton are digested much more quickly than insects (Dodson and Egger 1980), but most observations of tundra foraging adults and chicks indicate they certainly do prey heavily on chironomid adults taken from vegetation at the borders of pools.

The most detailed summer diet data are from Barrow and the northern Chukotski Peninsula, Siberia (Table 4).

Table 4. Diets of Red Phalaropes.

Barrow, June-July 1965-1969, n=56. Data of S.J. T. McClan, Jr., summarized in Tracy and Schamel (1981).

N. Chukotski Peninsula, Siberia, June-July 1970, n=41. From Kistchinski and Chernov (1973).

	<u>Barrow</u>	<u>Chukotski</u>
Larval tipulids	58%	12%
Adult tipulids	1	3
Larval chironomids	10	17
Adult chironomids	16	41
Beetles	6	14
Other insects	8	10
Other: spider, zooplankton, etc.	1	3

They show the greatest dependence on chironomids, and at Barrow, larval tipulids. Both sets of data are averages over the breeding season, and obscure the inevitable seasonality in diets in response to seasonality of available prey. Differences in seasonal composition of the bird samples may account for some of the greatest differences between the samples. Manniche (1910) found principally adults and larvae of gnats (probably chironomids) in stomachs of Red Phalaropes during the breeding season in northeast Greenland, and Mayfield (1978) reports spiders and chironomids in the stomachs of this species breeding on Eathurst Island in the Canadian arctic. He states that adults took mainly chironomid larvae in the early breeding season, switching to almost exclusively chironomid adults when these emerged in July. Young phalaropes gathered adult midges at pond edges.

After breeding, females begin southward migration from the tundra in late June and early July. Adult males frequently move to coastal lagoons, saltmarsh pools, and shorelines in late July and early August (Connors et al 1979). Fledged juveniles flock along ocean and lagoon shorelines, near sloughs, and in saltmarsh pools. Diets near Barrow include some chironomid adults, but consist principally of a wide variety of zooplankton (calanoid copepods, amphipods, euphausiids, decapod zoea, chaetognaths; Connors and Risebrough 1976, 1977, 1978; Connor et al 1982). At Simpson Lagoon, juvenile phalaropes fed on amphipods, copepods and mysid shrimp (Johnson 1978).

Dunlin. Diets of this species have been studied extensively, principally near Barrow. In June and August they prey most heavily on tipulid larvae on the drier portions of coastal tundra, but in July they feed on emerging adult tipulids in these habitats and move to marshier areas with their chicks to feed on emerging adults and larvae of chironomids (Table 5: Holmes 1966b, Holmes and Pitelka 1968). Data in Table 5 show these marked seasonal changes in diets of both adult and young birds. The importance of chironomids in Dunlin diets is exaggerated by these figures, which are percent by number of prey items. When converted to percent of biomass, the small size of chironomids relative to tipulids results in a decrease in their implied importance. For example, during the July 21-30 period the 50% chironomid component in Table

Table 5. Diets of **Dunlinat** Barrow. Percent composition by number of items. From Holmes (1966b).

A. Adults, n=364.

	June 1-10	June 11-20	June 21-30	July 1-10	July 11-20	July 21-30	July 31 Aug 14	Aug 15-29	Summer Average
Larval tipulids	71%	81	65	8	8	9	15	51	39%
Adult tipulids	0	0	0	40	17	8	0	0	8
Larval chironomids	7	3	3	24	61	74	78	41	36
Adult chironomids	0	0	0	21	7	5	1	0	4
Beetles	1 1	10	18	6	5	4	3	6	8
Other insects	8	4	10	2	2	1	1	1	4

B. Juveniles, 1959-1963, n=181.

Larval tipulids				1	2	0	4	4	2
Adult tipulids				26	29	11	1	0	13
Larval chironomids				0	26	35	83	93	47
Adult chironomids				63	30	15	1	0	22
Beetles, other insects				6	5	18	10	1	8
Spiders				4	4	18	1	0	5

5 represents less than 10% of the biomass of the diet for that period. On a biomass basis, Dunlins foraging on the tundra depend heavily on tipulids, either larvae or adults, throughout the summer.

A sample of 29 Dunlin collected on the tundra near Churchill, Manitoba over three summers also fed more heavily on tipulid larvae than on other prey (Baker 1977). At another Alaskan site, Kolomak River in the Yukon-Kuskokwim Delta, Holmes (1970) analyzed stomachs of 131 adult Dunlin over three summers and found much heavier dependence on chironomids than at Barrow. At Kolomak, Dunlin nest in an extensive marsh, with less upland (tipulid) habitat than at Barrow, but with very high densities of chironomids. Dunlin diets consisted of 85% and 50% chironomid larvae early and late in the breeding season, with a switch to 11% chironomid larvae and 50% chironomid adults in mid-season during insect emergence.

In August and September, many Dunlin remain on the tundra, as indicated by Table 5, but others, adults and juveniles, forage in littoral areas. In saltmarshes, on mudflats, and at edges of sloughs and lagoons, these birds prey predominantly on chironomid larvae. In seven adults and 28 juveniles collected in late summer in these habitats at coastal sites from Cape Prince of Wales to Lonely, Alaska, 27 birds (77%) contained almost entirely chironomid larvae. The remainder contained amphipods, isopods, euphausiids, beetles, oligochaetes and seeds (Connors and Risebrough 1976, 1977, 1978, 1979). Some birds also forage on beaches, taking a variety of crustaceans.

Pectoral Sandpiper. ---- This species at Barrow has a remarkably similar diet to that of Dunlin (Pitelka 1957, Holmes and Pitelka 1968). Table 6 shows an almost identical seasonality to the diet, changing from tipulid larvae in June to adult insects in early July and then to chironomid larvae. Converted to biomass figures, the data in Table 6 would show that this species, like the Dunlin, is heavily dependent on tipulid larvae throughout the summer.

Table 6. Diets of adult Pectoral Sandpipers at Barrow, n=204. From Holmes and Pitelka (1968). Percent by number of items.

	June 1-10	June 11-20	June 21-30	July 1-10	July 11-20	July 21-30	July 31 Aug 14	Summer Average
Larval tipulids	73%	80	66	9	9	10	16	38%
Adult tipulids	0	0	0	45	16	7	2	10
Larval chironomids	8	4	3	30	61	75	80	37
Adult chironomids	0	0	0	27	6	4	1	5
Other insects	19	14	31	7	6	4	1	12

Young Pectoral Sandpipers also have diets similar to young Dunlin (Holmes and Pitelka 1968). From a sample of 130 birds collected over five summers, diets consisted primarily of adult tipulids and chironomids in July after hatching, shifting primarily to chironomid larvae in late July and August. Tipulid larvae were important only in early August.

Northern Phalarope.----- Available diet information for this species is not as extensive as for the Red Phalarope, but their prey seem to be similar. Chironomid larvae and emerging adults were the most frequent prey in Canada (Baker 1977) and in Finland (Hilden and Vuolanto 1972). At Churchill, Manitoba, 24 birds had fed on adult chironomids (45% by number) larval chironomids (21%) beetle adults and larvae (20%) and adult tipulids (9%). Three adults collected on breeding grounds near Cape Krusenstern, Alaska in early June all contained insect parts, primarily chironomid larvae and adults (Connors, unpublished). Unlike most other shorebirds, the chicks must depend initially on emerging adult insects, mainly chironomids, which are easily taken from the surface of vegetation. After fledging, juvenile Northerns move to shoreline areas as described for Red Phalaropes; diets in these habitats

shift to marine and brackish water plankton (Connors, unpublished).

American Golden Plover. ---- No detailed analyses of diet have been published for this species on arctic Alaskan breeding grounds, but several scattered observations indicate that, as with the other shore-birds, insects are the principal prey. The diet probably does contrast with that of sandpipers, however, since this species is more restricted to the drier, more sparsely vegetated upland tundra. Bent (1927) reports that Hantzsch found them eating beetles and caterpillars on Baffin Island in Canada, and several observers have noted that berries of Empetrum and Vaccinium are taken on breeding grounds. On the Pribilof Islands, Preble and McAtee (1923) found mainly beetles, with some *flies* and other insects, as well as seeds, in two stomachs.

On Prudhoe Bay tundra, tipulid larvae may be important to this species also. The similar Golden Plover (Pluvialis apricaria) of northern Europe fed principally on larvae of tipulids and other dipterans (50% of biomass of animal prey) and on adult beetles (33%) and larval beetles (7%) in Norway, where Byrkjedal (1980) examined 101 stomachs. In May and August, Empetrum berries comprised about 30% and 40% of the total diet, but in June and July they were not taken. American Golden Plovers at Churchill, Manitoba (Baker 1977) had fed on berries, dipteran larvae, snails and adult beetles. In August, juvenile American Golden Plovers near Kotzebue Sound, Alaska, feed in saltmarshes as well as on tundra, taking chironomid larvae and berries (Connors and Connors 1982), but along the Beaufort coast they remain in the drier tundra habitats (Connors et al 1979).

Baird's Sandpiper. ---- This is the fourth of the common sandpipers studied at Barrow by Holmes and Pitelka (1968). Stomach contents from 60 adults are summarized in Table 7. Tipulid larvae, and to a lesser extent chironomid larvae, are important in June, after which birds switch to emerging adults of both groups in July, continuing to take adult chironomids in early August, later than other Barrow sandpipers. They also take more beetles and spiders in July and August compared to other sandpipers. Baird's Sandpiper chicks take mainly adult chironomids at first, switching to beetles, spiders, chironomid larvae and col-

lembolids (springtails) in late July and August.

Table 7. Diets of adult Baird's Sandpipers at Barrow, n=66. From Holmes and Pitelka (1968). Per cent by number of items.

	June 1-10	June 11-20	June 21-30	July 1-10	July 11-20	July 21-30	July 31 Aug 14	Summer Average
Larval tipulids	34%	56	40	22	8	0	0	23%
Adult tipulids	0	0	4	9	16	17	4	7
Larval chironomids	53	23	5	17	7	36	36	25
Adult chironomids	0	0	16	37	48	20	23	21
Beetles	7	17	7	3	20	20	37	16
Spiders	0	4	8	3	6	8	0	4

Buff-breasted Sandpiper. ---- No diet analyses have been published for this species on breeding grounds. However, its mode of foraging (surface pecks on vegetation and dry ground) and its nesting habitat (dry, upland tundra) suggest these prey: tipulid larvae and (in July) adults, beetles, and spiders. Chironomids are probably less important to this species, although chicks may prey on them heavily at times.

Diets of the remaining four shorebirds and one passerine listed in Table 1 as nesting at low densities on the study area are less well known than several of the common species already discussed. All evidence, however, suggests a similar range of foods, with insect prey, especially tipulids, chironomids, and beetles. Ruddy Turnstones at Ellesmere Island in Canada took plant matter very early in the breeding season, but switched to insects, mainly adult chironomids and larvae of chironomids and tipulids, as these became available (Nettleship 1973). Silt Sandpiper stomachs from Canada contained mainly larvae of tipulids and chironomids and plant seeds (Baker 1977). Long-billed Dowitchers in July and August, foraging in saltmarshes and mudflats near Kotzebue

Sound and at Barrow, contained 88% chironomid larvae (n=13; Connors, unpublished). During the breeding season on tundra their diets may be more diverse. Snow Buntings take a range of insects and plant seeds similar to Lapland Longspur diets (Parmalee 1968).

The obvious conclusion from these diet studies is this: monitoring populations of only tipulid and chironomid flies will provide a meaningful assessment of food conditions for almost all the most common species of the tundra bird community near West Road. Adding adult beetles to this list would probably cover the most upland and most distinctive foragers, the Golden Plover and (perhaps) Buff-breasted Sandpiper, as well. This extreme lack of diversity in diets of the nine most common species in a community is *unusual compared* with temperate and tropical areas; it affords the possibility of relatively easily monitoring food resources for most of the tundra avian community.

IV. POSSIBLE EFFECTS OF WEST ROAD ON FOOD SUPPLIES OF TUNDRA BIRDS.

West Road and its associated disturbances have the potential to affect populations of insects upon which tundra birds depend. The principal effects have been discussed at length in Troy and Johnson (1982), Webber et al (1982), MacLean and Ayres (1982) and Everett (1982), and will be summarized here. I separate them into three main categories and several subdivisions.

1. Activity disturbance
2. Gross habitat changes
 - A. Gravel
 - B. Impoundments
 - (1) vegetation, soils, and water cover
 - (2) tundra invertebrates
3. Lesser habitat or phenology changes
 - A. Dust
 - (1) vegetation and soils
 - (2) snow melt
 - (3) tundra invertebrates
 - B. Snow melt
 - (1) vegetation and soils
 - (2) tundra invertebrates

1. Activity Disturbance.

The first category refers to the noise and commotion associated with road use, and may have negative effects on nesting densities of some birds, especially the larger waterfowl and avian predators. At present we have no reason to expect any direct effects on populations of tundra invertebrates, except as these might be altered if their bird predators are excluded from areas *close* to the road. Since in this *report* we are interested only in effects of altered prey densities on bird densities, we can ignore road activity disturbance effects.

2. Gross Habitat Changes.

A. Gravel. ---- Covering tundra with gravel is the most obvious habitat change observed, and the effect is easily measured, since the

covered tundra is **lost** as bird nesting habitat. Effects on insect populations are similarly drastic, but there are no secondary effects on (the missing) birds arising from the lost insects, so we can **also ignore** gravel in this report.

B. Impoundments. ---- Changes in drainage patterns will have profound effects on soils, vegetation and water cover at affected sites, and **these will** affect *several* aspects of insect ecology, as **well as** suitability for nesting and foraging by different bird species. Connors and Risebrough (1979) reported some changes measured in bird use of an altered drainage site near West Road. Insect species at each point with altered drainage may also change. For example, the tipulid fly Tipula arctica inhabiting dry habitats (MacLean et al 1982) may be replaced by the tipulid Pedicia hannah as these become wetter, or by any of several species of chironomids if they become permanently water covered. With or without species changes, the densities of larva **may** change in response to the **changing** conditions of vegetation, moisture and detritus accumulation which can result from drainage changes. Phenology of insect *emergence* might also be **affected, by** retaining ice cover **or** cold water cover until later in the season. Finally, the availability of insects to shorebird predators will certainly be affected, since impounded waters **may** exceed the depth at which shorebirds can forage (only a few centimeters for some species). Other, more direct effects of impoundments on bird populations include the loss of potential nest sites and the loss of foraging areas for many species (longspurs and shorebirds) but the potential enhancement of foraging for waterfowl.

The road probably also affects *insects* and birds on the side of the road opposite the impoundment, since the loss of water drainage across some of the tundra **may** alter vegetation and insect populations. Changes are **likely to** be less severe, however.

Road impoundments differ from natural ponds in some respects. First, the fluctuations between high and low water conditions can be greater with impoundments, which may drain efficiently later in the season when culverts are ice free and snow melt has ended. The completeness of drainage depends on the size and placement of road culverts. This fluctuation would affect vegetation and insect populations in the rather broad "drying zone" around the margin of the impoundment. So-

cond, natural tundra ponds have usually reached stable conditions with respect to vegetation and insect communities, as well as microtopographically; most ponds have relatively narrow, sometimes abrupt, borders with the adjacent drier tundra. Impoundments will remain in a state of flux with respect to these characteristics for several years or perhaps decades. In particular, newly inundated areas, even with stable water conditions, cannot acquire stable insect populations in one or two seasons if Butler et al (1980) are correct that tundra chironomids have life cycles lasting up to seven years.

One final point concerning impoundment effects: Not all changes in bird populations will be negative. On transects in a road-impounded area not far from West Road, Connors and Risebrough (1979) found briefly elevated waterfowl densities in early June but much lower shorebird densities throughout the breeding season. By August, however, the area had drained considerably and was much more heavily used by post-breeding and migrating shorebirds than was a control area nearby. The impoundment reduced breeding densities but provided a desirable late season foraging habitat.

3. Lesser habitat or phenology changes.

A. Dust and B. Snow Melt. ---- Dust from gravel roads, settling on the adjacent tundra, can alter soil chemistry and vegetation (see Everett 1982, Webber et al 1982). Soil texture and chemistry and plant production of detritus, together with water content, determine the environment of tundra invertebrates such as dipteran larvae. Any changes may affect insect populations by altering insect species or densities at each point.

Dust may also affect snowmelt by increasing solar heat absorption. This can produce earlier snowmelt in dusted areas, accelerating the phenology of insect emergence (MacLean et al 1982). In view of Holmes' (1966a, 1966b) argument that shorebird nesting phenology is determined by the need for emerging adult insects upon which chicks can feed, any changes in insect phenology might alter bird productivity. However, birds usually occupy early snow melt areas before later snow melt areas, and this alone may synchronize bird and insect phenologies. Another effect of roads may partially offset the early snowmelt caused

by dust. The road can act as a snow fence, resulting in deeper accumulation of snow near the road, where dust is also greatest. Date of **complete** snow melt might remain relatively unchanged, therefore, although an increase in local moisture might be the result. This in turn can **alter** characteristics of **soils**, vegetation and insect populations. It is **not** possible to predict the net effect on insect and bird populations.

V. FOOD AS A FACTOR LIMITING TUNDRA BIRD POPULATIONS.

The question of whether food limits bird populations has proven extremely difficult to answer for any species in spite of considerable interest by biologists for several decades. In this section I shall attempt a brief review of this question as it applies to tundra bird populations, and will consider some particular complications imposed by the migration cycles of arctic birds. The aim of this discussion is to develop the background for suggesting specific studies which would be helpful in analyzing potential effects of West Road on bird populations. This applied objective, as well as the time constraints involved in preparing the report, require that some topics must be treated summarily, drawing the most reasonable conclusions from published studies.

In this discussion I use the term "limiting factor" to mean a factor which exerts a density-dependent influence on bird populations such that populations increase at low density and decrease at high density. This produces a feedback loop: as bird densities increase, the limiting factor exerts a stronger negative influence, which reduces densities. As densities decrease, the negative influence decreases, and populations increase again. The net effect is an equilibrium density controlled by the limiting factor.

Lack (1954) summarized the principal reasons, all indirect, to believe that food limits bird populations in many cases: First, few adults are observed to die from predation or disease, the principal alternate density-dependent factors which might limit populations. There are exceptions to this, of course, but it is generally true of arctic-breeding shorebirds. Second, many studies have shown that birds are more numerous where food is more common, and some arctic bird data support this, as discussed below. Third, species where they coexist generally occupy different food niches, and niches are frequently narrower where close competitors are present or resources are less, suggesting that competition for food is important. Finally, birds of many species have been observed fighting for food (but this does not often apply to nesting shorebirds). Schoener (1968) considered variation in territory size among species whose food sources differ in kind, density and distribution, concluding that territory sizes (and therefore nesting den-

sities) *among* species vary depending on food distribution in the same way as has been shown for territory sizes within species. Both *relationships* suggest that food resources act as a limiting factor on bird densities within and between species.

Potential Limiting Factors.

We can consider the following factors as potentially limiting arctic tundra shorebird populations:

- (1) Disease
- (2) Habitat
- (3) Predation**
- (4) Food
- (5) Migration and Winter Requirements

I will discuss each of these briefly, and will present my reasons to discount the importance of the first three factors. Under the fourth factor, I will consider the possible mechanisms, as well as the different scales of time and area response of tundra bird populations to food as a limiting factor. This discussion may seem to digress more than is warranted, but I found the process of formulating this description useful in considering how this factor might operate on the tundra. Different scales of response to food limitation may have quite different results on local or widespread bird population densities. I will cite some studies which suggest that tundra food does limit bird populations. I will combine several processes under migration and winter requirements to consider the evidence that arctic shorebird populations may be limited by resources away from tundra breeding grounds. Finally I will suggest a model which may reconcile these seemingly contradictory evidence concerning winter and summer resource limitation.

Disease. ---- This can probably be dismissed as an important **C z C** factor, although parasites have been noted in many shorebirds. Breeding populations never attain the densities likely to promote rapid transmission of pathogens, so this factor could only be included with (5), pertaining to the occasional concentrations of birds in winter or in migration. Even there, however, observations of disease-caused mortality are rare.

Habitat. - - - - That competition for habitat limits tundra bird

populations has been suggested by two removal studies at Barrow. In both Dunlin (Holmes 1966a) and Lapland Longspur (Seastedt and MacLean 1979), territories from which residents were removed were quickly occupied by new displaying males, suggesting that the new males had previously been prevented from occupying territories by a shortage of suitable habitat. However, the main attributes provided by habitat are food, cover from predation, especially of nests and chicks, and space to breed unmolested by conspecifics and competitors. Successful breeding has been noted in tundra species whose nesting densities vary widely from year to year (Myers and Pitelka 1980, Custer and Pitelka 1977, Holmes 1966b) or from place to place (Holmes 1970, Seastedt and Maclean 1979), so space per se is probably not limiting. Nest sites are also unlikely to limit densities, since the ground nests of shorebirds and longspurs typically occur in spots whose physical attributes are repeated frequently even over small distances of tundra. Thus, if habitat is limiting, it is probably because it provides food or cover from predation, and these factors are considered separately below.

Predation. ---- Predation is frequently important, accounting for more than half the eggs and young lost in studies of Lapland Longspurs and shorebirds (Jehl 1971, Custer and Pitelka 1977, Seastedt and Maclean 1979). However, Jehl (1971) found no evidence that predation acted as a density-dependent factor. This may be so because many arctic predators take bird eggs and young as alternates to their main lemming prey (Maher 1970, Custer and Pitelka 1977). Predation may account for some temporary bird population changes (Custer and Pitelka 1977) but does not appear to be the principal limiting factor.

Food. ---- Food is a very plausible factor limiting tundra bird densities, as suggested by previous authors (Holmes 1966a, MacLean 1969). Food might limit populations in several ways differing in scale of time and area response, as well as in mechanism, but all these ways require some kind of balance between available prey densities and nesting bird densities. Consider the possible scales of time response:

(a) Bird densities may adjust within each season to changes in prey availability. This does not appear to be the case, since nesting densities are determined at initiation of breeding in June. Subsequently, unpredictable weather may depress or increase availability of sea-

sonally variable prey (MacLean and Pitelka 1971), with consequent effects on nesting success and productivity. Nesting densities, however, do not appear capable of sudden increases after mid-June, since the brief season requires a fairly rigid phenology of nesting. Some nests fail, however, and while some second efforts occur, the time available for these is short, and in general nesting densities decline during the season.

(b) In each year bird densities may be based on the availability of food during the same year. This requires birds to assess food availability at the beginning of the summer, when, along the Beaufort coast, much of the potential foraging area is still inaccessible due to ice and snow cover. Further, some foods such as chironomid larvae often remain inaccessible because of water cover until July (MacLean and Pitelka 1971). Thus for early settling birds such as Dunlin and Lapland Longspur this mechanism seems unlikely, but for the later arriving nesters, especially Pectoral Sandpiper, such an assessment may be more useful. Pectoral Sandpiper densities, in fact, are much more variable between years at Barrow than are these other species (Pitelka 1959). A comparison of insect and bird densities between 1962 and 1963 at Barrow showed a sharp increase in densities of tipulid larvae in 1963 and an even sharper increase in nesting densities of Pectoral Sandpiper, although Dunlin densities remained constant (Holmes 1966a).

(c) Bird densities may be determined each year by prey densities in the preceding year, probably through changes in bird productivity. But productivity in a particular year is strongly affected by the predator regime or weather within that year and may vary widely from year to year for reasons other than food densities. Thus it would be difficult for a close correspondence between food density and next year nesting density to be maintained.

(d) Bird densities may be based on "average" prey densities over several years. This may be a weighted average, giving greater importance to some densities than to others. As an example, years of minimum food densities may be much more important than mean densities in determining long-term bird population densities, as suggested by Wiens (1977) for the general role of "ecological crunches" in shaping interspecific competition. In the highly variable resource con-

ditions of arctic tundra, I suggest that neither the lowest nor the highest food availability years figure overwhelmingly in this average. When food is extremely scarce, as it would be if weather inhibits insect hatches when sandpiper chicks depend on this food, productivity may drop to near zero. Under these severe conditions, productivity is not sensitive to nesting density; it is extremely low for all densities. Similarly, in years of extreme food abundance success will be high for a wide range of nesting densities. Thus the number of very bad or very good years matters, and is measured by an average, but the degree of badness or goodness may have little effect past some threshold levels.

Two mechanisms may match bird densities to "average" prey densities:

(1) By individual assessment of habitat quality. The mechanism implied here again requires assessment of average or potential prey densities by nesting birds, but now the assessment is based on characteristics of habitat. This assessment capability might be genetically controlled, since it could be under strong selection pressure, or it might to some extent be learned by birds with prior breeding experience. In species with some degree of philopatry (site faithfulness: for example Dunlin and Semipalmated Sandpipers: Holmes 1966b, Safriel 1971, Norton et al 1975), it might also depend on prior familiarity with a particular site. On a small area scale, Seastedt and MacLean (1979) found that Lapland Longspur territory size was only weakly correlated inversely with insect density within the same year, but was more strongly correlated with average insect densities over several years. They suggest the birds assess the potential value of the habitat, and that competition in areas of good habitat (and good average or 'expected' insect abundance) results in smaller territories and higher local nesting densities. This same mechanism could operate over larger areas. If food is ultimately limiting, this assessment mechanism must be coupled with a feedback mechanism based on productivity.

(2) By changes in bird productivity. This mechanism does not require the same active role of individual assessment. Briefly, areas of good food densities produce more young birds and result in higher densities of nesting birds in subsequent years. The area scale of this response depends partly on the degree of philopatry of adults and their

offspring. This feedback mechanism based on bird productivity is discussed in more detail in a subsequent section.

Over what scales of area response may food be limiting to tundra bird populations?

(a) By territory size within one site. On this small scale, climate is fairly constant and communities of prey species and bird species do not vary within single habitats, but territory size may be adjusted to food densities, as in the Lapland Longspur example (Seastedt and MacLean 1979). At another site with a different climate and different communities of plants, insects, birds, predators, etc., territory size would also be adjusted to prey densities, but on a distinct local scale.

(b) On a scale of kilometers. At each site (such as Barrow or Prudhoe Bay), the mix of habitats and probably the food density within habitats varies over this scale, as microclimate (temperature and precipitation) changes. Average bird densities may vary over this scale, limited by mean food densities over the same scale.

(c) Between sites (10's or 100's of kilometers). On this scale, there may be major climate differences, bird community changes due to species geographic distributions (which alter the intra- and inter-specific competitive environment), and changes in insect communities, phenology, and predator distributions. These factors may all affect the relationship between food density and bird density when we compare areas as distinct as Prudhoe Bay and Barrow.

Holmes (1970) measured Dunlin nesting densities and insect densities at Barrow and at the Kolomak River in the Yukon-Kuskokwim Delta. The comparison is complicated by differences in insect communities, habitat structure and phenology at the sites, but ratios of insect larval densities at the Kolomak River site to insect larval densities at Barrow varied between 16 at the beginning of nesting to 1.6 at fledging. Dunlin nesting densities averaged 5 times greater at the Kolomak River. The comparison is further complicated by differences in numbers of competing insectivorous birds at the two sites but Holmes concluded that differences in Dunlin densities were related to differences in food availability and that territoriality functions to disperse the bird populations in relation to their food. At Barrow, Holmes (1966a) removed

Dunlin from territories by shooting, and new birds occupied these *terri-*
tories almost immediately up to 20 June. This suggests competition for
resources, probably food, with territoriality maintaining low densities.

The data generated by prior studies at Barrow and Prudhoe Bay
permit a limited comparison of bird and prey densities at these coastal
sites. Norton (1975) estimated total energy consumption of the Prudhoe
Bay insectivore community to be only 75% of the comparable figure for
Barrow because of lower bird densities at Prudhoe Bay (3×10^5 kcal·
 $\text{km}^{-2} \cdot \text{yr}^{-1}$ vs. 4×10^5 at Barrow). MacLean (1982) compared the overall
tipulid biomass at the two sites ($41.6 \text{ mg} \cdot \text{m}^{-2}$ at Prudhoe Bay, $54.9 \text{ mg} \cdot$
 ul^{-2} at Barrow) and found a similarly lower value of this important food
item at Prudhoe Bay (76% of Barrow density). These values, based on
only two or more years do not account sufficiently for the variability
in bird and prey densities to give more than a hint of a causal re-
lationship. As data from additional years' study become available we
may be able to see whether this relationship is maintained. Other po-
tential factors discussed above may have played a role in producing low-
er Prudhoe Bay bird densities however.

In summary, food may limit tundra bird nesting densities over a
wide range of area scales, from individual territory sizes to geographic
sites. On a time scale, it is most likely to operate on "average" den-
sities of insects and birds over several years rather than on shorter
time scales. The mechanism of limitation might be through changes in
bird productivity, perhaps mediated by territorial behavior.

Species Differences in Demography.

For a closed system involving a local population of one or sever-
al similar species, a productivity feedback system can operate very
simply and directly, and a model to demonstrate this is developed below.
This suggests the probable mechanism for food limitation of tundra bird
densities, and is therefore a useful exercise, but the actual situation
in the arctic is made more complex by marked differences between species
in demographic characters such as annual variability in numbers at a
site, or individual philopatry (site faithfulness). For example, Dunlin
densities remain fairly stable between years at Barrow, and individuals
tend to return to the same, or nearby breeding areas in subsequent sea-

sons (Holmes 1966a). If Dunlins only compete for food intraspecifically, then increases in Dunlin densities will increase competition. But Pectoral Sandpipers share the same food resources, yet this species is much more variable in numbers, and *not* strongly philopatric (Pitelka 1959, Holmes 1966a). Pitelka et al (1974) consider the Pectoral Sandpiper an opportunistic species which changes its distribution between years, probably in response to changing resource distributions. Changes in nesting density at a site may be determined by resource conditions at sites away from the one in question, however. Thus a closed system treatment is not strictly appropriate, and the "averages" of food density and bird density at a site must account for these additional fluctuations due to independently changing competitor densities.

Productivity Feedback Model.

Consider a simplified tundra system in which birds prey on a single type of food present at maximum density at the beginning of each season. Food density is progressively reduced through the season by bird foraging. Assume further that prey items are uniformly distributed over a single continuous habitat.

MacLean (1980) estimated rates at which tundra birds must obtain prey during the breeding season to meet the needs of successful nesting. These rates vary depending on available daily foraging time, size of adult birds, size of prey, and nesting duties, and range for some common species from about 1-10 per minute for large Tipulacarinifrons to 20-100 for chironomids. Thus there is a minimum prey density, P_m , below which birds cannot gather food at a rate R_m sufficient for successful nesting. Over the entire breeding season, this R_m translates into F_m , the minimum amount of food required per successful nesting attempt. Since in our model all the prey are present at the beginning of the season, a bird nesting density of B requires at least an available prey density of $P = B \times F_m$. But the birds can only take a fraction of the total prey present because a portion P_u of the total prey density is unavailable (due to topography, vegetation, depth and substrate characteristics), and because below the prey density P_m the foraging rate R_m necessary for successful nesting cannot be maintained. The initial prey density required is therefore

$$P_o \geq P_m + P_u + P \quad , \quad P = B \times F_m$$

P_m and P_u are set by factors of habitat and physiology, so for any density P_o , there is a maximum B which permits successful nesting. If B is below this maximum, all birds can gather the required food F_m for successful nesting, and bird productivity is high. The population density B therefore increases in succeeding seasons. As B increases beyond the limit P set by $P = P_m + P_u + p$, then F_m must decrease, and productivity drops. In succeeding seasons B decreases until birds can again gather F_m , and productivity then increases. Thus the feedback loop based on food limiting nesting density is complete. In fact, productivity may adjust over a range of values from very low (zero) to very high, depending on how closely P and B correspond each season.

This simple view allows some obvious corrections to our assumptions. First, since prey populations vary considerably from year to year (as do other non-food factors which affect productivity) the productivity-based feedback will not operate smoothly from year to year. However, if bird densities are below or above the limits set by average prey densities over several years, the changes in productivity should gradually accumulate to alter the resultant bird densities.

Second, since food densities are never uniform over all areas, we can consider the effects of a model with food contained in many equal discrete patches. Instead of gradually reducing prey density through the season, the effect of foraging will be to reduce the number and density of patches. F_m , the total food needed for successful breeding, requires that each nesting attempt acquire a certain number n of patches. Below a minimum patch density p_m , search time to locate a patch would be too great for successful nesting, so this patchy model is analogous to the prey item model, with patch density treated as prey item density: $p_o \geq p_m + p$, with p (the patch density above minimum p_m required for successful nesting) dependent upon the density of foraging birds. so, with either a uniform or a patchy prey, the initial food density determines the bird nesting density which will be successful, and average bird population density adjusts to average prey density by changes in productivity.

Migration and winter requirements. ---- The final category of potential limiting factors includes the hazards and requirements of migration and wintering grounds. Some of these (e.g. weather) may be responsible for considerable bird mortality and may depress bird populations below the nesting densities which produce food limitation, but are not density-dependent and cannot be considered the factors limiting populations over the long term. However, disease, predation or food on wintering grounds or during migration may limit populations to average sizes below the food-limited carrying capacity of tundra nesting areas. These populations might then show effects of tundra food shortage in only very poor years. Changes over the upper range of tundra food densities would have little or no effect on average bird densities.

Holmes and Pitelka (1968) found broad diet overlap during much of the summer among four congeneric sandpiper species breeding at Barrow and warned that competition among sandpipers may be more severe on wintering grounds, where the evolved differences in bill morphology result in more distinct ecological segregation. Baker (1977) found close similarity in summer prey size and diets of ten shorebirds breeding near Churchill, Manitoba and concluded this indicated relaxed competition in the presence of abundant resources. This would argue against food limitation in summer. In contrast, several studies have found distinct foraging habits, habitats and diets among wintering shorebirds (Recher 1966, Couch 1966, Baker and Baker 1973). Baker and Baker (1973) believe this indicates greater competition for food in winter, and suggest that food is more likely to be limiting in winter than in summer. Their arguments are quite plausible, but the problem of population control in species undergoing such severe shifts in location, habitats, diets and community relationships several times each year is extremely complex. None of these authors has proposed a way of reconciling these apparently contradictory results suggesting resource limitation on both summer and winter grounds.

Limitation in Winter and in Summer: A Schematic Model.

I will suggest a model which may reconcile these different mechanisms. Much of the initial apparent contradiction of limiting factors

operating on both summer and winter grounds stems from a simplified view of these situations as representing the same, closed population unit. If all birds of species A nest at one density set by a resource limitation factor LF_s on the summer tundra and all birds winter at one density set by a resource limitation factor LF_w on winter grounds, both factors can be controlling populations only when the mean densities set by LF_s and LF_w correspond. If winter populations are controlled by LF_w at a level below the population densities permitted by LF_s , then LF_s has no effect; summer densities can never increase to their permitted limit set by the summer resource because LF_w limits the population below this size.

In fact densities of each species vary throughout its range on summer and winter grounds, as well as in migration. If local populations move between seasons as constant subpopulations, breeding, migrating and wintering together, the quandary might still exist. Evidence is accumulating of a high degree of site faithfulness in some shorebirds to breeding grounds (Handel, pers. comm., Holmes 1966b, Safriel 1971, Norton 1975) and to winter grounds (Kelly and Cogswell 1979, Myers et al 1979). However this does not necessarily imply constancy of subpopulations between seasons. An alternate model has individuals from one breeding group disperse over a wide range of winter grounds, and vice versa. A banding study of Black Turnstones nesting on the Yukon-Kuskokwim delta and wintering in California suggests that this may be the case, (Handel, pers. comm.). In this case, local breeding populations may occur at widely different densities adjusted to local resource limitations, but these populations in winter may spread over a broadly overlapping range, mixing with members of other local breeding populations. Thus changes in density at one local breeding site will have very little effect on winter population densities anywhere, and therefore do not evoke a strong response from any winter limiting factor. The operation of local winter and summer limiting factors are uncoupled in this model.

There remain the questions of the overall match of densities set by limiting factors, and which factors control population size next of the time. It should still be true that if the LF 's operate at densities which do not correspond at all between seasons, then only the more res-

trictive LF will have important effects. Considering a rather different system of migrant warblers nesting in north temperate forests and wintering in the neotropics, Morse (1980) suggests that compensating shifts in population density, distribution or ecological role by potential competitors in one season may arise when a species is limited primarily in the other season. This would tighten the competitive environment for the species within the previous non-limited season. The resultant "dynamic equilibrium" would act to equilibrate the limitation effects in both seasons.

We can guess that there have been some severe changes in competitive tundra shorebird environments within the past two centuries, as market gunning decimated populations of Eskimo Curlew, American Golden Plover and others, and as vast areas of coastal wintering shorebird habitat have been drained or filled. We do not know whether compensating changes by other species have operated to maintain a balance between competition on breeding and wintering grounds. We do know that populations of species such as American Golden Plover have recovered strongly since shooting stopped, indicating that they *were* not limited by resources in summer or winter during the recovery period.

There is a way to reconcile the operation of LF_w and LF_s without matching winter and summer densities closely. Figure 1 shows a hypothetical relationship between the strength of these factors as functions of bird densities. The density measurements would be expressed as birds per unit of limiting resource, adjusted for seasonal energy requirements. This is meant to relate the seasonal limiting factors to equivalent, but not necessarily equal densities, so that we may compare their effects between seasons.

The effects of LFs and LF_w may be very different. LF_s operates primarily through changes in productivity, while LF_w operates primarily through changes in survival of migrant and wintering birds. The shape of the LF curves in Figure 1 is meant to suggest that LF_w has a lower slope than LFs, but is not necessarily linear. The lower slope might arise because as food supply per bird decreases on winter grounds, birds can adjust by feeding longer, by changing habitats and prey, or by dispersing to other feeding areas. On breeding grounds, nesting birds are attached to a nest site, and can disperse only at the cost of lost pro-

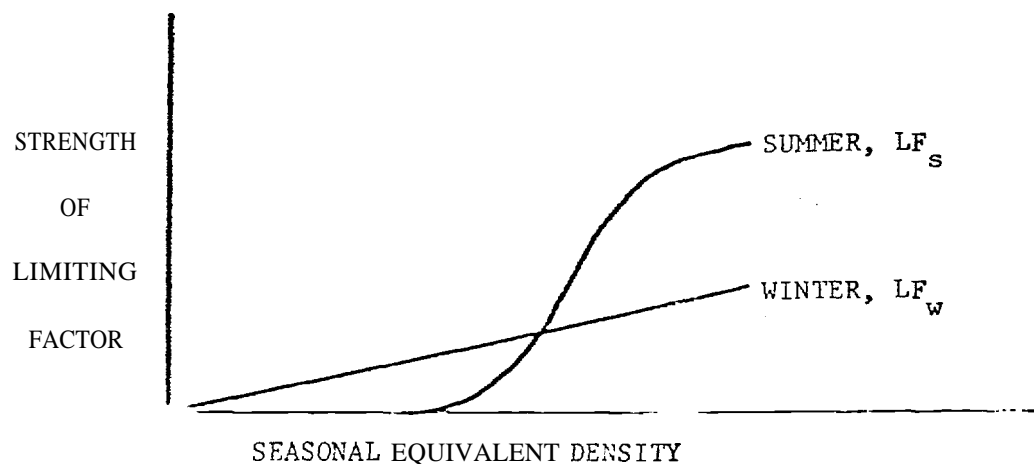


Figure 1. Hypothetical comparison of limiting factor responses.

ductivity; alternate prey are few; and newly hatched young are dependent on an *unpredictable* local food source. Thus if food supply per bird decreases, effects on productivity may be sharp.

Figure 1 suggests that over a broad range of densities, shorebird populations may be limited primarily by factors during migration and winter, but at high local breeding densities (or low resource levels) summer resources may be more important limiting factors. Birds might therefore evolve bill morphology and feeding strategies based on winter competition, but still face summer limitation under some conditions.

Another way of reconciling the evidence of more severe winter competition and of summer densities related to food supply depends on the differences in resource environments in winter and summer. Compared to the temperate tidal flat *wintering* areas of many shorebirds, the *tundra* food supply is extremely simple, lacking the diversity of prey available on winter grounds. The greater ecological segregation of shorebirds in winter (Recher 1966, Holmes and Pitelka 1968, Baker and Baker 1973, Mallory, pers. comm.) may merely reflect the greater diversity of potential prey in a competitive environment rather than increased competition on winter grounds. Faced with competition, shorebirds have evolved a variety of bill morphologies and foraging habits to use

the diverse and relatively dependable prey base permitted them to specialize in this way. With a simple but undependable, unpredictable prey base, such specialization would be too risky; the best strategy requires a generalist approach, so species overlap broadly in their diets. Food may be limiting on the average over many years because of its variability and unpredictability (Holmes and Pitelka 1968, MacLean and Pitelka 1971). In years of good food supply, birds experience very little competition. In years of poor food supply, competition may be heavy, but a narrower niche breadth is no solution because all birds must seek the same one or a few kinds of prey. The narrowed diet overlap among Earrow nesting sandpipers in late June and early July (Holmes and Pitelka 1968) is then a response to the slightly more diverse prey base during that period, rather than an indication of increased competition. In this view, competition in the presence of a diverse winter prey base has shaped the evolution of morphological and behavioral diversity among shorebirds, subject to the constraints of efficient foraging on the summer insect prey. This does not, however, imply that competition is more severe in winter, or that food is abundant and non-limiting in summer (contra Baker and Baker 1973 and Baker 1977). Food supplies, averaged over several years, may still be limiting to breeding birds of shorebirds.

VI. PROPOSED STUDIES

I have separated the central question of whether the West Road will alter bird densities by affecting densities of foods on which the birds depend into three more limited questions. First, what are the foods of the most common nesting birds along West Road? I believe this question has been adequately answered by previous studies, as reviewed in the first section of this report. The data are meager for some species, and moreover, have been gathered over many seasons at several arctic tundra sites, but the consistency of the *results* leaves little doubt of the central importance of larval and adult tipulid and chironomid flies. These are supplemented variously according to species and seasons with beetles and other insects, spiders, and plant material.

Road Effects on Insect Populations.

The second question to consider is that of the effects of the road on insect populations. A study of tipulid densities was begun in 1981 on the Waterflood Project, but would need to be expanded and continued before this question could be answered. First, chironomid populations must also be monitored, at least with emergence traps to sample emerging adults, and preferably with the addition of some benthic sampling of larvae at pond edges. This should be done at naturally occurring ponds as well as at impoundments caused by road construction. Measurement of larval populations at impoundment edges is especially important because these are drastically altered habitats which may change over many seasons until a stable flora and fauna are established. Tundra chironomid species, with life cycles of up to seven years (Butler et al., 1980), could not achieve stable populations in one season. Bird use of these habitats might continue to develop over several years.

The most profound effects of the road on insect populations will follow directly from any gross habitat changes produced. Alteration of drainage, resulting in temporary or permanent impoundments along the road, is the clearest example. As tundra is undisturbed, the environment of tundra insect larvae will change so drastically that species composi-

tion, not just densities, will be altered. Tipulid larvae in normally drained tundra will not emerge underwater. Phenology of emergence may also change, and availability of insects to foraging birds may be strongly affected. For example, any insect larvae beneath a water cover more than a few centimeters deep will be unavailable to small shorebirds unless they emerge and are blown to edges of the water, or unless the water drains or dries, exposing them to predation as the season progresses. Gross habitat changes such as impoundments are likely therefore to exert the most profound influences on bird populations, and should be monitored closely.

I agree in general with the recommendations for further study in MacLean (1982):

- (a) The sampling array should be placed closer to the road: 20m, 50m, 150m and control seem appropriate.
- (b) Habitats of all comparison plots in a series should be more closely matched by microhabitat as well as general topographic features.
- (c) Sampling should be expanded, preferably by addition of study plots, to allow averaging of densities over more of the habitat variation.
- (d) Sampling should be expanded to measure adult chironomid (midge) emergence, as well as their larval densities at edges of impoundments and natural ponds.

Studies of insect populations such as these or the studies proposed below are essential to understanding any Food-related effects of West Road on shorebird and longspur populations.

Food Limitation of Bird Populations.

The third question is the most difficult to answer: Does food operate as a limiting factor to tundra bird populations, such that changes in insect densities will ultimately cause changes in bird densities? The evidence from previous studies, as discussed above, is far from conclusive, and the issue remains one of the most complex in ecology. Four approaches might yield persuasive evidence within the Waterflood project.

A. Correlations between bird and insect densities over different sites.

Most of the indirect evidence for food limitation in bird studies has been of this kind. By measuring bird and insect densities on a large number of plots of comparable habitat, averaged over several years, we predict that if food is limiting, areas of higher average food density should support higher average bird density. This approach would require large samples. To average densities over time, at least five years of data collection would be necessary. Numbers of study plots required would depend on the range of density values over all areas and the variation in density values over time, but ten to twenty comparisons of pairs of similar habitat plots, or one or more correlation series of at least ten plots of similar habitat would probably be necessary. Just measuring chironomid and tipulid emergence adequately (at perhaps forty to eighty points per ten ha plot) in at least twenty plots for five years would be a formidable undertaking. This approach is probably too costly for consideration.

B. Changes in densities over time on the same sites.

If West Road causes changes in insect densities, and insect densities limit bird densities, then bird densities should show corresponding changes, if we monitor both parameters over many seasons. This approach follows the plan of 1981 Waterflood Project studies, and has a significant advantage over the correlational approach: since densities are measured at the same sites each year, and comparisons are between years (or averages of several years) on the same plots, we avoid problems of assuring equivalency of habitat between plots. This reduces both the number of plots required and the number of insect samples spread over each plot. An appropriate protocol might monitor four plots (two ha each for insects) on bird transects in the control area, six plots on bird transects at 25 m from the road, six plots on bird transects at 75 m from the road, and six plots at 175 m from the road. On each plot, traps could measure insect emergence at four separate sites in each of four habitats: dry, moist, wet, and pond. Trap sites would remain the same (or adjacent) each year. This would still require 264 traps monitored each year for, ideally, five years before the road is built and for five years after road use becomes stable. Shorter periods

might also be useful, but natural annual variation will reduce the sensitivity of comparisons. Bird nesting densities would need to be monitored on the same schedule, along the 1981 transect array, or possibly an abbreviated version of that array. Bird densities would be measured over a greater number of plots, corresponding to the same distances from the road as with the insect plots. Possible results of this study are these:

(1) Insect densities and bird densities are not measurably different after road use. This result would tell us nothing about whether food limits bird densities, but it would yield the important information regarding degree or level of road use which produces no detectable effect.

(2) Trisect densities and bird densities both change in the same direction. Unless obscured by other correlated factors, this result would yield strong evidence that bird densities are matched to, and presumably limited by, food densities. It would also measure the degree of these changes associated with a measured level of road use.

(3) Only insect densities change; only bird densities change; or both change in opposite directions. All three results would provide evidence that bird densities are not matched to food densities over the measured ranges. The three results would suggest different effects of the road on insect or bird densities, and might prove difficult to interpret or to apply to future situations.

C. Experimental changes in insect densities.

This approach is the experimental version of the previous approach. Because we can't predict whether the road will alter food densities sufficiently to demonstrate any food limiting effects on birds, we experimentally depress insect densities on a series of plots established away from the road. Success would hinge on proper application of an appropriate insecticide which must have no effect on vegetation or on bird physiology, while causing mortality of insect larvae. We might aim for a series of six control plots, six plots with densities reduced by 50%, and six plots with densities reduced by 90%. Measurement would entail the same array of traps and censusing as in Approach B.

If the technical problems of insecticide use can be overcome,

this approach would strike directly at the question of food limitation of tundra bird populations. It is therefore appealing from the general point of view, potentially providing an important and basic understanding of the dynamics of tundra ecosystems. It would provide information which, coupled with measurements of road effects on insect populations, would lead to predictions of road effects on bird populations. It would, however, require more total sampling than approach (2) and would not be as efficiently directed toward assessing the immediate effects of West Road. It would not, in particular, account for changes in phenology of insect emergence which may result from the road.

D. Effects of bird density on chick growth rates.

This experimental approach could focus on one central facet of the limitation question: Since the breeding cycle of shorebirds is timed to provide a food source of emerging adult insects for shorebird chicks (Holmes 1966a, 1966b; Holmes and Pitelka 1968), is this the sensitive, limiting step in shorebird productivity? Are shorebird densities set locally by food limitations during this period? Holmes (1966b) argues that the time of hatching and early growth of young sandpipers (July) is the time when food shortages are most likely to occur and have the greatest effects on breeding sandpipers. If the density of chicks is high with respect to food density, will chick growth rates and eventual chick survival suffer?

A series of wire enclosures might be set up at several sites encompassing similar habitats. After shorebirds hatch, chicks can be easily caught and placed within the enclosures, with different densities of chicks in different enclosures. Insect emergence would be monitored within each enclosure, and chick weights measured each day. We would look for a reduction of growth rates at high chick densities. If growth rates decline at densities which might naturally be reached on the tundra, it would suggest strongly that available food for chicks is limiting shorebird densities by reducing shorebird productivity. This would be an important result of general significance which would be extremely valuable in evaluating potential effects of West Road on insect and bird populations.

This study would not require the five years or more of the other

studies because **it** focuses on a central mechanism rather than the *res-*ponse to changes which must be **averaged** over several years. It would probably require two short seasons to overcome some potential **experimen-****tal** problems. In particular, the enclosures must not attract increased predation; in fact, **it** would be desirable to eliminate predation losses. Enclosures would need to be **large** (about 0.1 ha), but could be constructed very simply. Other details would need to be worked out. **An alterna-****tive** approach to this experiment would incorporate the pesticide technique of Approach C, changing food densities within enclosures which have the same chick densities.

Considering the time and expense as well as **the** expected return in useful information, **I** recommend a version of Approach D, the enclosure experiment, coupled with Approach **B**, the restructured monitoring of bird and insect populations on **plots** which might be affected by West Road. These studies, combined **with** a thorough **monitoring** of effects of gross habitat changes (in particular the impoundments along the road) will adequately cover **the** most important aspects of West Road effects on shorebird and **longspur** populations acting through changes in food resources.

VII. APPENDIX: A MORE GENERAL APPROACH TO STUDIES OF ROAD EFFECTS ON BIRD POPULATIONS

An alternate approach to this entire problem of effects of roads may be beyond the scope of Waterflood project studies because it focuses on road problems in a general way. West Road is currently under extremely light use. If use remains relatively light, any potential effects of roads will be light and possibly undetectable within the limits of time and money available for studies. The conclusion of no significant effects of West Road will be justified and welcome. It will not, however, be a general conclusion applicable to other roads and should never be extended to roads with markedly different levels of use. This is especially true because there may be critical or threshold levels of use or associated effects (for example, dust), which alter the relationship between the disturbance and the environmental response. There may be no response (of insect densities or bird densities, for example) below a critical disturbance level, but above that level there may be a strong dependence of densities on degree of disturbance, or even a complete failure of nesting success.

If in the future conclusions are needed with more general applicability than the Waterflood Project West Road studies supply, a comparison across several roads differing in use levels would offer a potentially powerful approach. Study plots would be established and monitored along at least three roads (low, medium and high use) on sections lying in identical directions and at similar distances from the coast. Studies might then proceed as with the Waterflood Project, but all results which suggest road effects could be compared against a measure of road use. We could then predict the response of the environment to a proposed level of road use, and might determine threshold levels of these responses. This would provide an extremely useful predictive and management tool.

The principal difficulty in making these comparisons between sites is the elimination of confounding factors which might explain observed effects. The most obvious of these, which would be at the heart of multiple site studies (but is also relevant to present Waterflood Project studies, is the dependence of almost all biological factors on

habitat. Two approaches are possible: We can *try* to eliminate the habitat factor by comparing plots which are identical in habitat but which differ in the level of a disturbance factor which we are investigating, or we can mathematically compare sites which differ in habitat using multivariate statistics with extensive habitat measurements. The first approach is preferable only if we can select sets of plots with sufficiently similar habitat measurements to feel confident that habitat differences could not explain any observed trends. The insect data from the 1981 Waterflood Project were collected according to this design, but the habitat categories were not sufficiently detailed, and observed trends in the data were discounted as arising from unintended differences in habitat (MacLean and Ayres 1982).

In practice, it is always difficult to closely match the habitat of study plots established in different areas. A protocol could be established, however, to select plots on the basis of a limited series of habitat measurements to eliminate major differences. Analytical techniques might subsequently be applied to evaluate and subtract habitat-related trends if data sets are large enough.

These considerations are, of course, also applicable to comparisons of experimental and control areas. Since bird use of coastal tundra by shorebirds and Lapland Longspurs is so strongly associated with habitat characteristics (Myers and Pitelka 1980, Connors et al 1982, Troy and Johnson 1982), small differences in habitat between comparison areas can easily obscure any differences caused by factors associated with roads. Habitat measurements, or at least continued statistical use of the geobotanical map information, are therefore essential to these studies.

Multivariate statistical techniques can be a powerful alternative to well-matched sets of habitat plots, and have been used to measure habitat use differences among bird species and among sites in several arctic studies (Myers and Pitelka 1980, Connors et al 1982, Troy and Johnson 1982). Some approach of this sort would probably be required in these comparisons among different years.

The point of this discussion is merely to suggest the potential power of this comparative approach. It could provide more generally applicable estimates of the effects of road use, but probably at greater

initial cost. The more focused studies initiated in the first season Waterflood Project, and the studies suggested in this report, will more efficiently meet the specific objectives of determining the environmental effects of West Road.

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